

THE GENERA OF ERIOCAULACEAE IN THE
SOUTHEASTERN UNITED STATES¹ROBERT KRAL²

ERIOCAULACEAE Desvaux, Ann. Sci. Nat. XIII. 39: 45. 1828, "Eriocauloneae," nom. cons.

(PIPEWORT FAMILY)

Annual or perennial, monoecious (less often dioecious), diminutive or robust, stemless or caulescent, usually rosulate, scapose aquatic or wetland herbs, mostly of acidic waters and substrates. Rootstock a rhizome or caudiciform, the roots fibrous, spongy, or spongy-septate (diaphragmed), with simple or paired root hairs. Stems short or elongate (in the latter often spreading-ascending), repent or prostrate, the axis sympodial or monopodial, sometimes branching. Leaves mostly polystichous, usually in rosettes, sometimes in looser spirals in the elongate-stemmed species, in rosettes spaced along an elongate slender axis, or in involucre rosettes in compound-scaped species, mostly graminiform, linear-lingulate, parallel nerved, the bases usually broad, open, clasping, the stomata paracytic. Scape(s) simple or compound, originating from or toward rosette center, 1 to many, each arising axillary to a rosette leaf, enclosed at base by a tubular, distally open, spathe-like sheath, the scape axis terete, usually twisted, mostly few-to-many-costate, terminating in a single,

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The illustration of *Syngonanthus* was drawn for the Generic Flora in 1975 from dissections made by Kenneth R. Robertson. The liquid-preserved specimens used were collected by R. E. UMBER in Hillsborough County, Florida; herbarium material by Kral and Kral (6777; GH) in Hernando County, Florida. Living plants brought by George K. Rogers from Columbus County, North Carolina, were used to check various details.

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chaffy, involucrate, sometimes proliferative, buttonlike head, the involucre bracts usually spirally imbricate in few to many gradate series, the receptacle smooth or variously hairy or chaffy. Flowers (florets) imperfect, regular (actinomorphic) or irregular (zygomorphic). Sepals 2 or 3, distinct or variously fused, usually diverging from a stipelike base (part of an androphore or gynophore). Petals lacking, 2, or 3, evident as lobes diverging from a stipelike base (androphore or gynophore) or merely a part of a lobeless column. Stamens 2–4(–6), when 2 or 3 alternating with sepals, often unequal; filaments epipetalous or appearing to arise from the apex of an androphore when petal lobes are reduced; anthers introrse or versatile, 2- or 4-sporangiate, 1- or 2-locular, dehiscent longitudinally; pollen monosulcate, trinucleate. Staminodia present in some 2- or 3-merous flowers, then glandlike or peglike and sometimes fimbriate or variously cleft, rarely with a stipitate blade. Gynoecium syncarpous, 2- or 3-carpellate; style terminal, 2- or 3-branched, the branches simple or rebranched apically, in some species the stylar apex producing appendages alternate with style branches; ovary superior, raised on a gynophore, 3-locular, the ovules 1 in each locule, ventral-apical, pendulous, orthotropous, 2-integumented. Fruit a thin-walled, loculicidal capsule; seeds small, variously ribbed or sculptured, the embryo small, apical, the endosperm copious, mealy-starchy, with compound starch grains. TYPE GENUS: *Eriocaulon* L.

A large, mainly pantropic family of about 13 genera and at least 1200 species, with a distinct majority in the Neotropics and in the genera *Paepalanthus* Mart. (about 500 species), *Eriocaulon* L. (about 400), and *Syngonanthus* Ruhland (about 200). Under the assumption that reduction in ovule number and uniformly imperfect flowers constitute evolutionary advancements, a present and popular view is to place the family as derived from the Commelinales, but distinct from that order (cf. Cronquist; Hutchinson; Takhtajan, 1980; Thorne, 1983).

In the New World only five genera—namely (in order of number of species) *Eriocaulon*, *Paepalanthus*, *Lachnocaulon* Kunth, *Syngonanthus*, and *Tonina* Aublet—are known to occur north of South America; just three of these are found in the United States, with only *Eriocaulon* being represented outside the Southeast. Of the three, *Eriocaulon* is the sole representative of the subfamily Eriocauloideae, while *Lachnocaulon* and *Syngonanthus* are treated under the other subfamily, Paepalanthoideae Ruhland.

The family is mainly distinguished by its combination of rosulate and sheathed-scapose habit; vessels with simple or scalariform perforations in all organs; leaves with polystichous arrangement and open, clasping bases (true wetland or aquatic species often with lacunar tissue evident); vascular bundles of stem closed and bicyclic; cuneate proteinaceous inclusions in sieve-tube plastids; root hairs on most roots; monoecious [or dioecious] habit; flowers and involucre bracts and bractlets chaffy, the flowers crowded in tight spirals in involucre heads; perianth 2- or 3-merous, 1- or 2-cyclic, regular or irregular, usually valvate in bud and often with mealy pubescence, the petals distinct or variously connate, at base incorporated into an androphore or a gynophore; androecium of 2 or 4, or 3 or 6 stamens, often in the trimerous flowers with

3 staminodia or glands at tube apex; gynoecium variously raised on the gynophore, 2- or 3-carpellate, the ovary 2- or 3-locular, each locule with a single ventral-apical, pendulous ovule; style branches 2 or 3, sometimes rebranching at stigma level [in many species producing appendages from the apex of the stylar column]; and fruit capsular, thin walled, loculicidal, the seeds small, with copious mealy endosperm and a tiny lateral-apical embryo.

Trichomes in most species are many and varied on all or nearly all organs. These may constitute at once the most neglected and the most useful taxonomic characters.

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KEY TO THE GENERA OF ERIOCAULACEAE IN THE
SOUTHEASTERN UNITED STATES

- A. Lacunar tissue evident at leaf bases; larger roots thickened, septate, appearing articulated and unbranched; perianth parts in 2's [3's in the Asian adventive *Eriocaulon cinereum*], each petal adaxially glandular; stamens (3 or) 4(–6), the anthers 2-locular,

- staminal column apically with 2 or 3 glands at center; carpels 2, style branches unappendaged, 2 [carpels 3, style branches 3 in many western, tropical American, or Asian species]. 1. *Eriocaulon*.
- A. Lacunar tissue not evident at leaf bases; larger roots either fibrous and evidently branched or thickened and fleshy (and then appearing neither septate nor branched); perianth parts in 3's, the petals if present eglandular; stamens 2 or 3, the anthers 1- or 2-locular, apex of staminal column usually with 3 appendaged or unappendaged glands; carpels (2 or) 3.
- B. Roots dark, slender, fibrous, evidently branched; scapes smooth or hairy, the hairs neither swollen nor glandular apically; expanded inflorescence globose or short-cylindrical, the outermost involucrel bracts reflexed and obscured by the rest of the inflorescence; trichomes of perianth tips clavate; staminal filaments fused to rim of an androphore, the anthers unilocular; style branched with bifid stigmas. 2. *Lachnocaulon*.
- B. Roots pale, thickened, spongy, appearing unbranched; scapes hairy, at least some of the hairs swollen at base, often glandular distally; expanded inflorescence hemispheric, outer bracts not obscured by the rest of the inflorescence; trichomes of perianth tapering, acute, not clavate; staminal filaments separating from corolla toward apex of tube, the anthers bilocular; style branches undivided. 3. *Syngonanthus*.

Subfamily ERIOCAULOIDEAE [Ruhland]

1. *Eriocaulon* Linnaeus, Sp. Pl. 1: 87. 1753; Gen. Pl. ed. 5. 38. 1754.

Rosulate, scapose, often tufted herbs, the roots evidently cross partitioned, the stems short or elongate, sometimes sparingly branched. Leaves linear-lingulate, often attenuate, gradually or abruptly flaring toward a clasping base, there often noticeably lacunar and pale, greener and less distinctly lacunar distally, the chlorenchymatous part of leaves increasing with extent and duration of emergence. Inflorescences scapose, the usually fluted scape encased at base by a tubular, fluted, distally open, often bifid or trifid sheath and terminating in a single hemispheric to globose or short-cylindrical, involucrel head, all parts chaffy and imbricate in several to very many tight spirals. Involucrel bracts in gradate spirals, hardly (if at all) longer than flowers, usually broad, green, gray-green, or paler, at least the margins translucent; receptacle trichomiferous, chaffy, or smooth. Sepals 2, scarious, usually equal, fused to a stipelike base, pale or colored, often translucent, navicular, frequently covered toward tips with farinose or translucent, multicellular trichomes. Petals mostly 2, fused at least toward bases, equal or unequal, similar to sepals but generally narrower, shorter, separated from them by a pronounced tubular stalk (partly petal and, in staminate flowers, partly stamen) and distinguishable from them by a dark gland on adaxial distal surface of each; outer and sometimes inner surfaces or margins frequently with multicellular, translucent or opaque trichomes; distal end of staminate perianth tube concave, sometimes with 2 or 3 dark glands at its center like those on corolla lobes. (Sepals and petals 3 [in the Californian *E. microcephalum* and] in the Asian adventive *E. cinereum*.) Stamens 3 or 4 to 6, 2 or 3 opposite the petals, the anthers introrse, dorsifixed and usually versatile, bilocular, tetrasporangiate, well exerted from the inflorescence at anthesis. Carpels 2, the ovary on a gynophore, 2-locular, the style

2-branched (carpels 3, locules 3 in *E. microcephalum*, *E. cinereum*). Pericarp thin, often velumlike, the style persisting. Seeds ovoid, ellipsoid, or broadly fusiform, variously lined, ridged, or papillate. LECTOTYPE SPECIES: *E. decangulare* L.; see Britton & Brown, Illus. Fl. No. U. S. & Canada, ed. 2. 1: 454. 1913. (Name from Greek *erion*, wool, and *caulos*, stalk, from the wool at the base of the scape in the original species, *fide* Arthur Stanley Pease in Fernald (1950).)—PIPEWORT, BUTTON-RODS, HAT-PINS (Small).

About 400 species, mostly pantropic, with a few representatives extending to temperate or boreal-transitional climates in both Asia and eastern North America, and only one (*Eriocaulon aquaticum* (Hill) Druce) in northern Europe (the Hebrides, Scotland).

Of the ten species reported for the United States and Canada, one (*Eriocaulon cinereum* R. Br.) is Asian, now sporadically established in rice-growing parts of California and Louisiana; another (*E. microcephalum* HBK.) is disjunct from the montane Neotropics and has been collected only once from southern California; and two (*E. aquaticum* and *E. Parkeri* B. L. Robinson) are principally of Pleistocene-glaciated latitudes in the eastern or central United States and Canada, each with extensions southward along the Appalachians or the coast into the southeastern United States. The remainder either center in the Coastal Plain of the Southeast with a few extensions into contiguous areas or are endemic to it; of these, only *E. decangulare* extends to (or is extended from) the Neotropics; not surprisingly, this is perhaps the most ecologically ample of our species.

Of the three southeastern genera in the Eriocaulaceae, *Eriocaulon* has the largest number of truly wetland or aquatic species and the most anatomical characters associated with an aquatic habit.

As to soil or soil-water reactions, all species except *Eriocaulon Parkeri*, usually in tidally influenced, circumneutral or even brackish sites, and *E. Ravenelii* Chapman, which favors wetlands transitional to brackish marsh, are found in acidic wet sites, such as pine flatwoods, low savannas, acid pond shores and shallows, sphagnous seeps and bogs, and seeps or pools on or around arenaceous rock. Of these, *E. decangulare* appears to be the most drought tolerant and is commonest in the drier transitions to wetlands.

Harold N. Moldenke, the world authority on the family, treated 43 species for the *North American Flora* (1937); a clear majority are comparatively narrow endemics, some still unknown beyond the type or a few collections. Since trichome characters and the relative dimensions of accrescent parts tend to vary considerably within well-known species, it is quite possible that a bio-systematic overview will be more conservative.

Of the three genera that occur in the Southeast, only *Eriocaulon* has nectariferous glands. Insect visitors are rare. It could be assumed that, for our species, the most common agent of pollination is wind.

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Subfamily PAEPALANTHOIDEAE Ruhland

2. *Lachnocaulon* Kunth, Enum. Pl. **3**: 497. 1841.

Annual or perennial, rosulate, scapose, often tufted herbs, the roots branched, slender, fibrous, with paired root hairs; perennation by lateral offshoots or short ascending rhizomes. Rosette leaves linear, acute or attenuate, in very flat spirals toward the apex of a short or elongate, sparingly branched stem, the bases

clasping, crowded, none of the leaf evidently lacunar, often hairy with slender, multicellular, translucent hairs; old leaf bases persisting as scales on stems. Inflorescences with scape base in a tubular, costate, apically open sheath, this hairy like leaves; scapes usually several, from axils of central rosette leaves, slender, twisted, variously costate, often with trichomes, terminating in a small (1 cm broad or narrower), white, gray, gray-brown, or brown, globose to ovoid or short-cylindric, involucrate head, each comprising an outer involucre of few to many spirally imbricate series of bracts and an inner bracteate, spirally imbricate mass of bracteate, chaffy, imperfect flowers, both staminate and carpellate. Receptacle of head covered by pale or yellowish, multicellular, filiform trichomes and by the floral bracts (1 or 2 per flower), these mostly about the size of involucral bracts, often navicular or strongly convex and with a few translucent or opaque, usually clavate, multicellular trichomes at the tip. Sepals 3, nearly distinct, similar to receptacular bracts, smooth or sparingly clavate-hairy. Petals lacking or reduced to hairs or small scales. Stamens 2 or 3, elevated on a tubular androphore at least as long; filaments linear; anthers oblong-linear, bisporangiate, unilocular, yellowish or pale, dorsifixed, introrse or versatile, exerted from heads at anthesis; staminodia (2? or) 3, lance-ovoid or peglike, often with fimbriate appendages. Gynoecium on a short, usually comose gynophore, 3-carpellate, the ovary 3-locular, 3-ovulate (2-merous in *L. digynum*); styles (2- or) 3-branched, the stylar column appendaged at apex, with appendages similar to those of staminate flowers. Fruit and seeds like those of *Eriocaulon*. TYPE SPECIES: *L. Michauxii* Kunth (*Eriocaulon villosum* Michx.) = *L. anceps* (Walter) Morong. (Name from Greek, *lachnos*, wool, and *chaulos*, stem, in reference to the long, soft, upwardly pointed hairs on the scapes of the type species.)—HAIRY PIPEWORT, BOG BUTTONS.

Seven species confined to the southeastern United States and Cuba. This small genus evidently centers in the Coastal Plain of the Southeastern States, with two species (*Lachnocaulon cubense* Ruhl. and *L. Ekmannii* Ruhl.) endemic to Cuba.

Our *Lachnocaulon* and *Syngonanthus* species inhabit ecologically drier sites than most species of *Eriocaulon* within the Coastal Plain, the physiographic province in which all the species occur. The optimum habitat is an acid, sandy, or sandy-peat-loam soil, usually one with a gley horizon and therefore saturated much of the year, but definitely one in which water does not stand except during the wettest periods. Soil and soil-water reaction are distinctly acid. *Sphagnum* is the most commonly associated bryophyte. All species appear to be best adapted to moist ecotones around acid wet areas, with the most diminutive species, *L. digynum* Koern., tolerating the wettest—and *L. anceps* and *L. Beyrichianum* Spohl. extending into the least moist—sites. Root systems within the genus are shallow, fine, and diffuse; the roots are septate and with paired, elongate and delicate hairs, providing a good adaptation to drier situations.

Both staminate and carpellate flowers develop peglike, often cleft or fringed appendages apically, in the former case on the androphore and alternating with the filament bases and in the latter alternating with the style branches. In the carpellate flowers, petals are reduced to three clumps of trichomes arising from



FIGURE 1. *Syngonanthus*. a-p, *S. flavidulus*: a, flowering plant, leaves decumbent from the basal rosette, showing sheaths at bases of peduncles, $\times \frac{1}{2}$; b, sheath enclosing base of peduncle, $\times 12$; c, flowering head at beginning of anthesis, bracts of head and anthers of staminate flowers visible, $\times 12$; d, detail of peduncle just below head, showing indumentum of divergent glandular trichomes and adpressed, simple ones, $\times 24$; e, uniseriate, septate, glandular trichome, $\times 100$; f, portion of head in vertical section, anthers of staminate flower and styles and petals of carpellate flower projecting above bracts, 2 bracts in section at extreme right, $\times 24$; g, staminate flower, the calyx lobes connate below, pubescent above, the petals united, vertically folded around the filaments, the anthers exerted, $\times 40$; h, upper portion of staminate flower in vertical section, showing rudimentary, 3-lobed gynoecium, $\times 40$; i, adaxial surface of anther, $\times 50$; j, carpellate flower, free petals (see "l") projecting beyond pubescent calyx lobes, tips of 3 stigmas protruding between petals, $\times 40$; k, head in fruit, carpellate flowers in concentric bands, $\times 6$; l, fruit partly enclosed by persistent petals (calyx lobes removed), showing seed through opening in 1 locule of capsule, $\times 50$; m, fruit, perianth removed, styles

the gynophore above the sepals. Stamens provide yet another distinguishing feature, the anthers being bisporangiate but one-locular at anthesis.

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Under family references see KRAL and MOLDENKE (1937); under references for *Eriocaulon*, see KRAL and MOLDENKE (1956).

3. **Syngonanthus** Ruhland in Urban, Symbol. Antill. 1: 487. 1900.

Low [to moderately tall, slender to coarse, solitary to] densely caespitose, [annual or] perennial, monoecious [or dioecious], rosulate herbs, the stems short [to very elongate], the primary roots mostly thickened-porous, pale, esep-tate, the branch roots much more slender, angular, with paired root hairs. Stems short [to elongate, sometimes branched]. Leaves mostly slenderly linear, smooth or variously hairy, often recurved, mostly firm and not evidently lacunar. Scape(s) solitary or many, from axils of inner rosette leaves, each enclosed at base by a tubular, open-ended, costate sheath, slender, terete and smooth or variously costate and hairy, erect or declinate, simple and arising directly from a basal rosette [or 1 or more times compound, each secondary or subsequent whorl subtended by an involucre or "rosette" of bracteal leaves comparable to but progressively smaller than those of the basal rosette, or scapes proliferative and substoloniferous, glabrous to sparsely or copiously pubescent, usually pilose and with sharp- or gland-tipped hairs often mixed with shorter, glandular ones]. Heads globose, urceolate, turbinate, or hemispheric, with many involucre bracts, these pale, papery-chaffy, imbricate in several tight, flat spirals, often gradate, shorter or longer than florets. Receptacle of heads pilose to subglabrate, the hairs elongate, sharp tipped, mostly silvery. Flowers trimerous and nearly regular. Sepals mostly chaffy and pale, distinct to near base, there comprising the outer part of the column (androphore, gynophore), smooth or with long hairs comparable to those of receptacle. Petals subequal; in the staminate flowers much more connate, the androphore a pronounced stipe, at the apex flaring into a cuplike, funnelform or clavate, concave-apexed corolla, the rim of which is often 3-toothed; in the carpellate with 3 blades departing from the gynophore and connate or connivent above at the level of the ovary or higher. Stamens 3, the filaments adnate to corolla at apex of androphore, alternating with 3 central glands at its concave center and opposite the lobes of its flaring rim (corolla limb), exerting the anthers beyond them; anthers 2- to 4-sporangiate, bilocular, the locules basally divergent. Ovary trilobed, tricarpellate, the gynophore shorter than the androphore of staminate flowers, the style elongate [or short, clavate], at apex with 3 elongate-linear, papillose stigmatic branches [their bases alternating with stipitate-bladed or

connate below and above but free in middle, seed visible through slit in capsule, $\times 50$; n, fruit in diagrammatic vertical section, seed pendulous from apical, axile placenta, endosperm evenly stippled, embryo unshaded, $\times 50$; o, seed, funiculus above, micropyle below, $\times 100$; p, same in vertical section, endosperm evenly stippled, seed coat and embryo unshaded, $\times 100$.

simple peglike, bearded appendages, or these lacking.] Capsule and seeds as in *Eriocaulon*. LECTOTYPE SPECIES: *Eriocaulon umbellatum* Lamarck (= *Syngonanthus umbellatus* (Lam.) Ruhland). (Name from Greek *syngonos*, joined together, and *anthos*, flower, from the connate petals of the carpellate flowers.)

About 200 species in Africa, the West Indies, and Central and South America, the earlier-described ones placed in various sections of *Paepalanthus*, subsequently transferred to *Syngonanthus* by Ruhland (1900). The center for these is the planalto of Brazil. In the Neotropics the genus becomes progressively less well represented northward. In North America north of Mexico, there is only *S. flavidulus* (Michx.) Ruhland (*Paepalanthus flavidulus* Kunth), shoe-buttons, bantam buttons, a caespitose plant with rhizomes slender, ascending; rosette leaves narrowly linear, acute, strongly recurved, often with a scattering of pustular-based, uniseriate, multicellular hairs; scapes numerous, pilose-glandular, wiry, erect or ascending, to 30 cm long; heads pale whitish yellow, chaffy, hemispheric, ca. 5–10 mm broad; receptacles densely translucent-pilose; androphores and gynophores hairy at the base; staminate corollas broadly funnelform, with 3 broadly triangular lobes; and carpellate corollas with 3 narrow lobes connivent over the ovary, with the slender stylar apex unappendaged.

Syngonanthus flavidulus is one of the commoner associates of most *Lachnocaulon* species, usually in sandy-peaty bog ecotones, flat, exposed sandy washes and seeps, and savannas and flatwoods in the lower Coastal Plain from eastern North Carolina, south through Florida, and west in the Gulf Coastal Plain to northwestern Florida and contiguous Alabama.

While this species agrees with many of the tropical ones in the character of its androphore (which appears as a long, pedicellike stipe) and in its cuplike or funnellike corolla with a triglandular center, it differs from most in having staminate flowers with densely pubescent sepal tips, carpellate flowers with a hairier gynophore and petals connate only at the base, and an unappendaged stylar apex. Interpretation of the evolution of species in this now very large genus is best left to those tropical botanists who work within its centers of diversity, particularly Brazil.

Many of the tropical species of *Syngonanthus* and *Paepalanthus* are both large and showy; the ones with larger and papery heads produce effects much like the “everlastings” (e.g., *Helichrysum* Gaertner, *Anaphalis* DC.) and are commercially exploited for dried plant decorations.

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